Isotopic analysis of the ecology of herbivores and carnivores from the Middle Pleistocene deposits of the Sierra De Atapuerca, northern Spain

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A B S T R A C T

Carbon and oxygen isotope values reveal resource partitioning among the large mammal fauna from three contemporaneous Middle Pleistocene hominid-bearing localities within the Sierra de Atapuerca (northern Spain). Carbon isotope values sampled from the tooth enamel of fauna present during Atapuerca Faunal Unit 6 show that a C_3-dominated ecosystem surrounded the area where fossils were preserved during this time. For the herbivores, Fallow deer isotope values are significantly different from Red deer and horses and show that this species did not forage in open environments at this locality. Red deer and horses show similar feeding strategies with less negative carbon values implying use of more open environments for these taxa. For the carnivores, carbon isotope values for *Ursus deningeri* are significantly different from either lions (*Panthera leo*) or foxes (*Vulpes vulpes*) and support the contention that this species is herbivorous. Special metabolic mechanisms involved in hibernation in *U. deningeri* might also have influenced its isotope values. The carbon isotope values of remaining carnivores were similar and suggest that each was typically a generalist carnivore, eating a wide variety of prey items. While the isotopic results generally correspond to ecology indicated by previous techniques, this study shows that isotope analyses can provide further insights that alternate techniques do not provide. Isotope analyses can help elucidate the ancient ecology of taxa present in the Sierra de Atapuerca during the Middle Pleistocene allowing for an accurate portrayal of the setting in which humans lived.

1. Introduction

The fossil deposits in the Sierra de Atapuerca of northern Spain (Fig. 1) have become well known due to the discovery of sustained presence of humans over more than the last one million years of the Pleistocene. Besides human remains and artifacts (Arsuaga et al., 1993, 2001; Bermúdez de Castro et al., 1997; Carbonell et al., 1995, 2001), abundant faunal remains have been recovered (Cuenca-Bescós and Conesa, 1997; García et al., 1997; García and Arsuaga, 1998, 1999, 2001b; van der Made, 1999, 2001; Cuenca-Bescós et al., 2001), providing the opportunity to examine community ecology through time (Rodríguez, 1997; López Antoñanzas and Cuenca-Bescós, 2002; García and Virgós, 2007), and attempt to understand the context in which humans lived over the time represented by the Middle Pleistocene deposits (Falguères et al., 1999; Bischoff et al., 2007) here analyzed.

One technique that has proven useful to examine faunal ecology in ancient mammals is through examination of stable isotope values found in tooth enamel (Quade et al., 1992; Bocherens et al., 1996; MacFadden and Cerling, 1996; Cerling et al., 1998; Koch et al., 1998; Bocherens, 2003; Drucker et al., 2003; Kohn et al., 2005). Isotopic analyses can reveal information about resource use and resource partitioning among fauna, being able to determine diet and habitat use, for example. While these analyses have concentrated on examining herbivorous taxa where there is a mixture of plants using the C_3 or C_4 photosynthetic pathways (DeNiro and Epstein, 1978a; Vogel, 1978; MacFadden and Cerling, 1996; Cerling et al., 1997; Koch et al., 1998), recent studies have shown resource use and partitioning among ancient carnivores as well as in areas containing only C_3 plants (Bocherens et al., 1996, 2004; Bocherens, 2003; Cerling et al., 2004; Kohn et al., 2005; Feranec and MacFadden, 2006).

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Fig. 1. Location of Sierra de Atapuerca complex of sites in northern Spain.

This study analyzes stable carbon and oxygen isotope values found in the tooth enamel of mammalian carnivores and herbivores with the overall aim of understanding the ecological context in which the ancestors of Neanderthals lived within the Sierra de Atapuerca during the Middle Pleistocene. We will address: (1) whether stable isotope values permit identification of resource use and partitioning among taxa? (2) If resource use and partitioning are determined, do the results corroborate the ecology predicted by other methodologies (e.g. morphology, comparison to extant species, and biometry)? We examine whether stable isotope analyses will provide another technique to better understand ancient ecology in the Sierra de Atapuerca which will enable an accurate portrayal of the setting in which humans lived.

2. Background

2.1. Locality correlation

The three archeo-paleontological sites from Sierra de Atapuerca included in this study can be divided into the Trinchera del Ferrocarril sites and the Sima de los Huesos site in the Cueva Mayor – Cueva del Silo karst complex (Fig. 2). The Trinchera del Ferrocarril includes the two sites: Trinchera Galería (TG) and Trinchera Dolina (TD). TD and TG have yielded fossil human remains, fauna, and lithic industries that range from the late Early Pleistocene to the Middle Pleistocene. However, for correlation reasons, this study only analyzes the faunas coming from the Middle Pleistocene layers of these two sites: Units GII and GIII of TG and levels TD10 and TD11 of TD. The Sima de los Huesos (SH) lies inside Cueva Mayor, and contains an extraordinary accumulation of a set of approximately thirty human individuals (*Homo heidelbergensis*) in an ancient mud-breccia, together with an assemblage of carnivores, especially bears (García et al., 1997; García, 2003) and scarce rodents and insectivores (Cuenca-Bescós and Conesa, 1997; Cuenca-Bescós et al., 2001).

The TG complex and TD are not currently connected to the Cueva Mayor – Cueva del Silo caves. SH has been dated to around 530 ka B.P. (Bischoff et al., 2007), while TGII-III and TD10-11 might be slightly younger, around 400 ka (Falguères et al., 1999; Berger et al., 2008) (Fig. 3). Even so, the three associations are referred to the same Faunal Unit (FU) (Cuenca-Bescós and García, 2007) and are characterized by the presence and/or absence of particular mammalian taxa. The three deposits share small (*Arvicola* sp., *Pliomys lenki*, *Clethrionomys* cf. *glareolus*, *Microtus (Terricola) atapuerquensis*, *Microtus (Microtus) arvalis*, *Microtus (Agricola) agrestis*) (Cuenca-Bescós et al., 2001) and large (*Dama dama clactoniana*, *Cervus elaphus priscus*, *Equus* sp. (caballine-type), *Hemitragus bonali*, *Panthera leo* cf. *fossilis*, *Vulpes vulpes*, *Meles meles*) mammals. Also, four horse teeth sampled for this study come from TD level 10, and were the same specimens sampled by ESR analysis providing a mean age of 372 ± 33 ka (Falguères et al., 1999) The fauna included in this study are placed within ATA FU 6 (Cuenca-Bescós and García, 2007), which is characterized by the presence of *Terricola atapuerquensis*, *Iberomys brecciensis* and *Allocricetus correzensis* (Cuenca-Bescós and García, 2007). ATA FU 6 is also represented by the presence of the caballine horses (*Equus caballus* ssp.), *Stephanorhinus* cf. *hemitoechus*, *D. dama clactoniana* and *H. bonali*. The first appearance of true wolves (*Canis lupus*) at Atapuerca also occurs within this faunal unit at GIII of TG. Similarly, the first appearance of *P. leo* at Atapuerca could be either at the base of TD10 or at TG or SH. This faunal unit likely represents the period of expansion of lions in Europe since they disperse into the continent from Africa in the Early Middle Pleistocene by their first occurrence at Isernia La Pineta (Italy) (García, 2003) dated by $^{40}Ar/^{39}Ar$ to 605 ka (Coltorti et al., 2005). Although the fauna from these three localities may have lived at different times, we suspect the ecological relationship among mammals within ATA FU 6 to have remained the same over time.

2.2. Faunal ecology and isotopic predictions

For many of the taxa sampled within this study morphology has not changed significantly since the Middle Pleistocene. To get a better understanding of the ecology of these more ancient populations, we review the dietary preferences of the extant species with the aim of more accurately identifying the paleoecology of fauna present during the Pleistocene around the Sierra de Atapuerca.

2.3. Herbivores

Cervids: *Cervus elaphus* (Red deer) is classified as an intermediate feeder by Hofmann (1985, 1989), and therefore is capable of feeding on a wide variety of forage including grasses, sedges and concentrate foods (e. g. leaves of trees and shrubs). More specifically, Gebert and Verheyden-Tixier (2001), identified the food resources of European *C. elaphus* and similarly concluded that they eat a wide range of plant species and select a mixed diet with four principal plant groups: grass and sedges ($\sim$30%, a very constant resource), *Calluna* and *Vaccinium* (heath family) ($\sim$23%, principally in moorland from Scotland), leaves of deciduous trees and shrubs ($\sim$10%, principally in mixed-deciduous forests) and conifers ($\sim$9%,

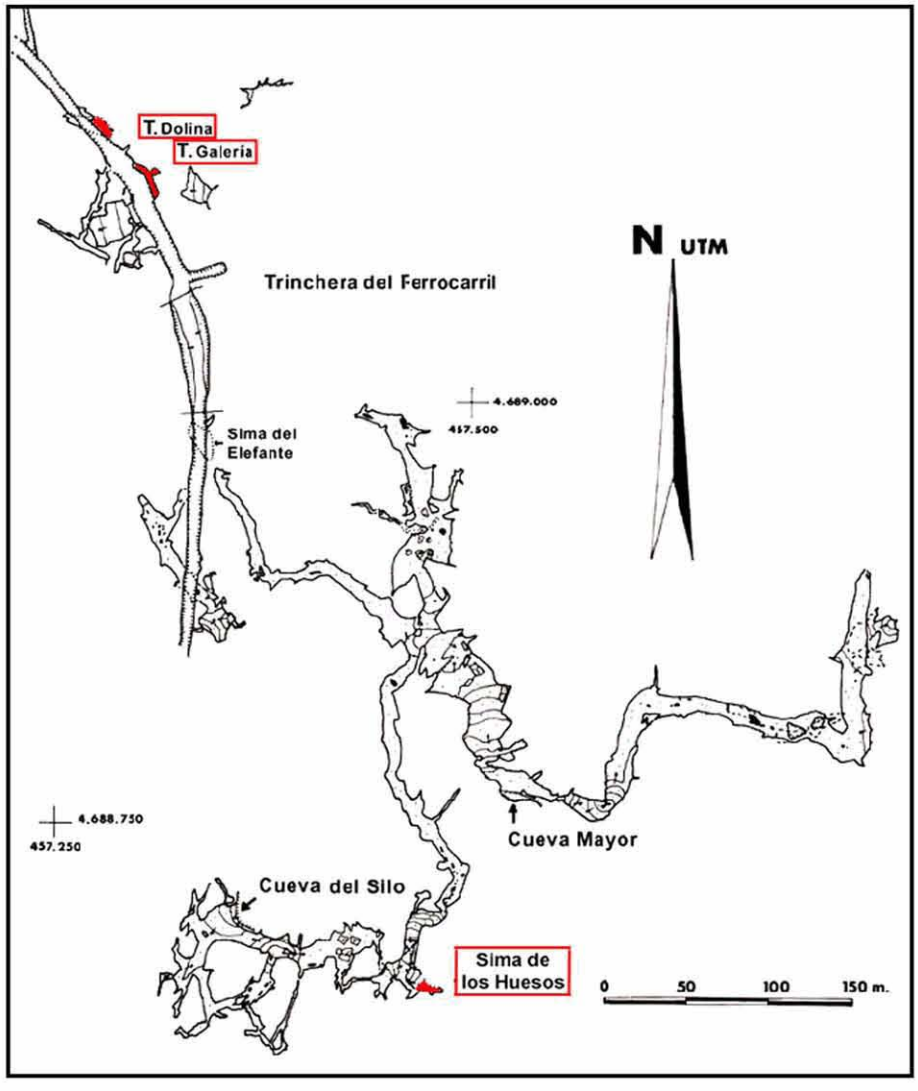

Fig. 2. Plan of the Sierra de Atapuerca cave systems (by G. E. Edelweiss).

in forests, particularly during winter and spring). When these mean percentages were analyzed in detail, it was evident that environmental factors, such as type of habitat and season affect the composition of European *C. elaphus* diet. For these cervids, it was only grasses and sedges that did not show any significant variation in consumption among habitats, seasons, or sexes, and generally always occurred at a relatively constant level. For the ancient *C. elaphus*, we predict carbon isotope values typical of an intermediate

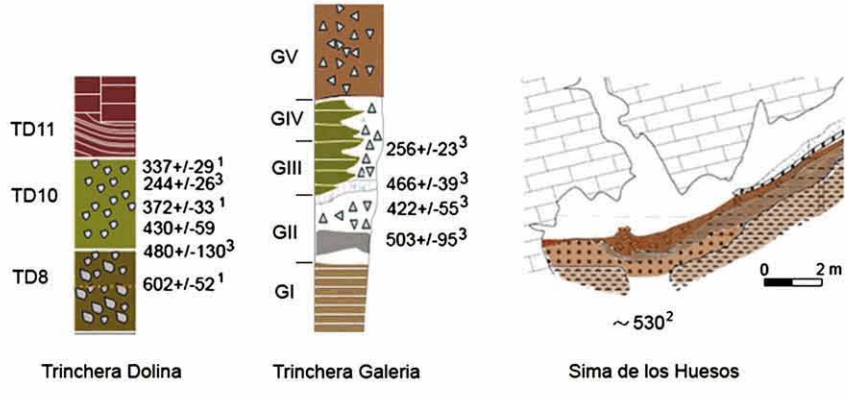

Fig. 3. The sites and layers from which samples derive. All sampled fauna are all included within the same local faunal unit (ATA FU 6). All dates in thousands of years before present (ka). [1]Dates from Falguères et al. (1999). [2]Dates from Bischoff et al. (2007). [3]Dates from Berger et al. (2008).

feeding herbivore with some individuals showing consumption of grasses in open habitats.

The present ecology of Fallow deer, *D. dama*, suggests that this species is well adapted to a wide range of different habitats in Europe. However, the origin of its modern generalized ecological ability might be the result of a high degree of environmental patchiness found in its post-glacial Near East range. It was from this range that the species was introduced to most of Europe (Apollonio et al., 1998). In present-day Spain, *D. dama* inhabiting Sierra de Cazorla, a Mediterranean habitat with evergreen *Quercus*, have a strong preference for grasses (García-González and Cuartas, 1992) although this population also consumes *Quercus rotundifolia*, *Phillyrea latifolia*, *Rosmarinus officinalis*, *Oryzopsis paradoxa* and *Festuca arundinacea* (Martínez Martínez, 2002). While grasses appear to be the dominant food for modern populations, *D. dama* have been known to consume a large proportion of browse, including fruit, during winter (Chapman and Chapman, 1975; Putnam, 1988). The 300–400 ka faunal assemblages at Quesem cave (Israel) (Barkai et al., 2003) display a high predominance of Fallow deer roughly correlative to the time period of the faunas analyzed here at Atapuerca. This suggests that *D. dama* was also a successful inhabitant of Mediterranean dry environments, at least during the Middle Pleistocene. Consumption of grasses would suggest competition with *C. elaphus*, while browsing implies a higher degree of resource partitioning between these deer species. During the Middle and Late Pleistocene, *Dama clactoniana* and *D. dama* have been identified at many sites, generally in temperate faunal associations (Kurtén, 1968; Leonardi and Petronio, 1976). Based on this, *D. dama* is suspected to inhabit open woodland and forest, being found mostly amongst woodland glades and openings. More studies of *D. dama* are needed, especially in mixed-deciduous and/or evergreen forest habitats, in order to get a better understanding of its ecology, today and in the Pleistocene. Even so, based on what we know of their modern and suspected ancient ecology (Bocherens et al., 1999; Geist, 1999), we predict that isotope values will be similar to *C. elaphus* showing the capability of feeding on an intermediate diet but having a strong preference for grasses and more open habitats. Isotopically, we would predict that *D. dama* would have values slightly more positive than *C. elaphus* indicative of preference of feeding on grasses.

Equids: The interpretation of ecology in ancient horse taxa differs based on their functional anatomy. The Caballine group, which first appeared in Europe at Mosbach, are typically characterized by larger molars and generally more massive extremities. This is in comparison to the smaller Hemionines, which are thought to inhabit more open and arid regions as modern Asian representatives. The *Equus* sp. teeth sampled here all belong to the Caballine clade (van der Made et al., 2003), and based on modern ecology and prior studies on ancient horses (MacFadden et al., 1999; Kaiser and Franz-Odendaal, 2004; Stevens and Hedges, 2004), we predict that the analyzed horses are intermediate feeders, foraging grasses as well as tree and shrub foliage where and when available. Further, we hypothesize that they would be more similar isotopically to *C. elaphus* than to *D. dama* at this fossil locality.

2.4. Carnivores

Ursids: One unique carnivore represented in the deposits of the Sierra de Atapuerca is *Ursus deningeri*. *U. deningeri* is the forerunner of the well-known Late Pleistocene cave bear, *Ursus spelaeus*, and is the most common bear species represented during the Middle Pleistocene in Europe. These two chronospecies, constituting part of the cave bear lineage, have a presumed hyper-specialization towards vegetarianism. While the phylogenetic relationship between the two cave bear species has been largely demonstrated by many morphological studies (Torres, 1984; Tsoukala, 1989; Mazza and Rustioni, 1994; Mazza et al., 1995; García et al., 1997; García, 2003) and recently through ancient DNA analyses (Valdiosera et al., 2006), the degree of vegetarianism in the ancestral *U. deningeri*, remains unexplored. Dental and cranial adaptations observed in *U. spelaeus* indicate an almost exclusively vegetarian habit (Soergel, 1926; Erdbrink, 1953; Thenius, 1965; Kurtén, 1968) and recent isotopic studies support this conclusion (Bocherens et al., 1991a, 1994). One of our primary aims will be to focus on the ecology of *U. deningeri* to better understand their evolution and the transition from the ancestral *U. deningeri* to descendent *U. spelaeus*.

The teeth of *U. deningeri* appear to be morphologically intermediate between *Ursus dolinensis*, the most primitive representative of the cave bear lineage whose dentition resembles *Ursus arctos*, and *U. spelaeus*, whose teeth are much broader (García and Arsuaga, 2001a, b). This implies that although the diet might not be exclusively vegetarian (as in *U. spelaeus)*, the dental anatomy is more similar to the "herbivorous" cave bears than to those of the more carnivorous brown bears (Mazza and Rustioni, 1994; García, 2003). Isotopic analyses should help elucidate this dietary ecology further. Based on previous carbon isotope analyses of bears (Bocherens et al., 1991a, 1994, 1997; Nelson et al., 1998), we predict the isotope values to be more negative than the other carnivores.

Canids: The Middle Pleistocene wolf from Atapuerca is considered a "true wolf" based on morphology even though morphological dimensions have not reached the slightly larger size of the modern Holarctic species, *C. lupus*. For the Atapuerca wolf, we presume a generalist-carnivore diet, with isotope values generally falling among the large herbivore (prey) values, similar to what modern wolves eat today in the wild (Mech, 1974). The dhole, *Cuon alpinus*, is known to primarily hunt and eat large mammals, although smaller mammals will be taken on occasion (Cohen, 1978). Due to the lack of the lower third molar, dholes are generally thought to be more carnivorous than wolves or foxes (García and Arsuaga, 1998). Similar to the other canids, the red fox, *V. vulpes*, is a generalist carnivore, but in contrast to the other sampled canids, the fox is known to take a large proportion of small mammals as prey as opposed to large mammals (Lariviere and Pasitschniak-Arts, 1996). Scavenging as well as consumption of various plant matter and invertebrates is not uncommon (Lariviere and Pasitschniak-Arts, 1996). Based on known canid diets, we would predict to observe carbon isotope values intermediate among the various prey for the sampled Atapuerca canids.

Felids: Modern *Lynx* spp. are strictly carnivorous and typically consume lagomorphs and other small mammals as their primary prey although larger prey (e.g., Roe deer) can be taken on occasion (Tumlison, 1987; Lariviere and Walton, 1997). Lions, *P. leo*, are opportunistic predators, and while they may occasionally hunt and consume small prey such as rodents, fish or even termites, they typically prey on large mammals (Haas et al., 2005). Isotopically, we would expect to find lion values similar to those of the large canids, intermediate among the sampled herbivores. We would expect the *Lynx* isotope values to be similar to the red fox, both being consumers of similar small prey.

2.5. Isotopes in Paleoecology

Isotopic results in this study are expressed in the standard δ-notation: $X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is the $\delta^{13}C$ or $\delta^{18}O$ value, and $R = {}^{13}C/{}^{12}C$ and ${}^{18}O/{}^{16}O$, respectively. The $\delta^{13}C$ and $\delta^{18}O$ values are reported relative to the V-PDB standard.

Animals that feed on different kinds of plants will reflect the carbon isotope value of their food in their tissues (DeNiro and Epstein, 1978b; Vogel, 1978; Tieszen et al., 1979). Carbon isotope values are useful in diet studies because the three different

photosynthetic pathways used by plants, C_3, C_4, and Crassulacean Acid Metabolism (CAM), impart different $^{13}C/^{12}C$ ratios to plant tissues. Tropical, warm-growing-season grasses and sedges using the C_4, or Hatch-Slack, photosynthetic pathway are relatively enriched in the heavy carbon isotope (^{13}C). These plants have a mean $\delta^{13}C$ value of −13.0‰ and generally range from −9‰ to −19‰ (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). On the other hand, C_3, or Calvin cycle, plants including most trees and shrubs, as well as grasses in regions with cool growing seasons, are relatively enriched in the light carbon isotope (^{12}C). C_3 plants have a mean $\delta^{13}C$ value of −27.0‰ and typically range from −22‰ to −35‰ (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). The third pathway, the Crassulacean Acid Metabolism (CAM) pathway, is characteristic of succulents (e.g. cacti) and may yield values that range between the end members for C_3 and C_4 plants (O'Leary, 1988; Ehleringer et al., 1991; Ehleringer and Monson, 1993). CAM photosynthesis is typically found in more restricted xeric habitats, CAM plants are generally not widespread on the landscape (Ehleringer et al., 1991), and very few extant large ungulates use succulents as a significant part of their diet (Janis and Ehrhardt, 1988). Therefore, it is assumed that the herbivores in this study did not make succulents a significant part of their diet, and the isotopic effects of CAM photosynthesis are not considered in this study.

Studies utilizing differences in the carbon isotope values from mammals generally focus on communities containing a mixture of C_3 and C_4 plants, which enables taxa to be distinguished based on the predominant forage included in the diet (Vogel, 1978; Tieszen, 1994; MacFadden and Cerling, 1996; Cerling et al., 1998; Koch et al., 1998; Kohn et al., 2005). Based on previous studies and where the fossil localities are situated, it is predicted that the flora during the late Pleistocene in the Sierra de Atapuerca was dominated by C_3 plants (Flynn et al., 1984; Collins and Jones, 1985; Sage et al., 1999; Pamlqvist et al., 2003). Different processes, however, such as variation in light intensity, temperature, nutrient availability, and water stress, can produce variation in the $\delta^{13}C$ value in C_3 plants (Farquhar et al., 1989; O'Leary et al., 1992; Ehleringer and Monson, 1993; Koch, 1998; Heaton, 1999; Bocherens, 2003). C_3 plants typically have more negative values in closed, forested habitats; while in more open, drier habitats more positive isotope values are typical (Farquhar et al., 1989; van der Merwe and Medina, 1991; O'Leary et al., 1992; Ehleringer and Monson, 1993; Heaton, 1999; Bocherens, 2003; Cerling et al., 2004). Recent studies have used these habitat differences to highlight the use of carbon isotopes in determining resource partitioning of herbivores in C_3-dominated environments (Quade and Cerling, 1995; Bocherens et al., 1997, 2001; Cerling et al., 1999, 2004; Bocherens, 2003; Drucker et al., 2003; Feranec and MacFadden, 2006).

2.6. Stable carbon isotope values in mammalian herbivores

Herbivores reflect the carbon isotope values of plants ingested, but the $\delta^{13}C$ value of the tooth enamel is further enriched by a consistent amount, about +14.0‰ for medium- to large-bodied mammals (Cerling and Harris, 1999; Passey et al., 2005). Setting the fractionation from plant material to tooth enamel at +14.0‰, extant taxa that feed solely on C_3 plants will display enamel carbon isotope values between −21.0‰ and −8.0‰. Modern taxa that feed solely on C_4 plants exhibit enamel $\delta^{13}C$ values around 0.0‰ (Koch, 1998; Passey et al., 2005). The carbon in plants and ultimately enamel is derived from the atmosphere. The $\delta^{13}C$ value of atmospheric CO_2 has decreased −1.5‰, from −6.5‰ to about −8.0‰, due to fossil fuel burning over the last 200 years (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992). A diet of pure C_3 plants would range from −19.5‰ to −6.5‰ in the enamel of Pleistocene herbivores. Isotope values more positive than −6.5‰ would imply incorporation of either C_4 or CAM plants into the diet. The −6.5‰ $\delta^{13}C$ value as indicative of C_4 or CAM plant incorporation into an herbivore diet appears very conservative as previous studies on modern and fossil herbivores show that pure C_3 feeders rarely have values more positive than −8.0‰ (MacFadden and Cerling, 1996; Cerling et al., 1999, 2004).

2.7. Carbon isotopes in mammalian carnivores

Similar to the herbivores, carnivore carbon isotope values within tooth enamel derive from the isotopic value of their prey. Based on the portion of prey ingested (e.g. muscle, organs), and the fractionation of isotopic values between the food and the tooth enamel, carnivores typically display tooth enamel carbon isotope values slightly more negative than the tooth enamel of their prey (Bocherens et al., 1994; Grocke, 1997; Lee-Thorp et al., 2000; Bocherens, 2000; Kohn et al., 2005; Fox-Dobbs et al., 2006). Fox-Dobbs et al. (2006) show a mean $\delta^{13}C$ difference from prey tooth enamel to predator tooth enamel of −1.3‰.

2.8. Oxygen isotopes in mammals

The oxygen isotopes in mammal tooth enamel depend on the isotopic composition of ingested water, the consistent fractionation of oxygen isotopes between body water and the tooth enamel, and the metabolism of the particular animal (Land et al., 1980; Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985; Koch et al., 1989; Kohn, 1996; Kohn et al., 1996, 1998). Mammals ingest water from two sources, either through drinking meteoric water or from what they consume. Meteoric water is affected by climatic influences such as temperature and humidity, such that $\delta^{18}O$ values are more positive where and when it is warmer and more negative where and when it is colder (Dansgaard et al., 1982; Rozanski et al., 1992; Fricke and O'Neil, 1996; Kohn and Welker, 2005). Because all the sampled species are located within the same general area at the same time, the isotopic values of ingested meteoric waters are assumed to be similar. For the herbivores, water in plant leaves also varies and is typically more positive than the local meteoric waters due to evapotranspiration. Enrichment in $\delta^{18}O$ values in the leaves is more pronounced in warmer and more arid conditions (Yakir et al., 1990; Yakir, 1992; Ometto et al., 2005). Thus, animals that occupy open habitats would be expected to ingest more positive $\delta^{18}O$ as compared to taxa foraging in a cooler, moister forested habitat.

Body size and metabolism can also influence the oxygen isotope composition in tooth enamel. Large mammals that are obligate drinkers and tend to have lower metabolisms are most likely to track $\delta^{18}O$ values of ingested waters (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). All species analyzed within this study are large and considered to have a lower metabolism. However, because it is not possible to know whether the ancient taxa studied were obligate drinkers or to know the metabolism of each individual, the $\delta^{18}O$ values are scrutinized with caution. Where appropriate, we will also make comparisons to a species' modern ecology and whether they are currently drinkers or capable of obtaining enough water from alternate sources (e.g., vegetation).

3. Materials and methods

Tooth enamel of a total of 58 specimens from nine species, representing the most abundant species in the assemblages, from the Middle Pleistocene deposits of the Sierra de Atapuerca was

sampled. The three herbivore species analyzed include *C. elaphus priscus*, *D. dama clactoniana*, and *Equus* sp. caballine-type. Six carnivore species were also sampled and include *C. lupus*, *C. alpinus*, *Lynx pardinus spelaeus*, *P. leo*, *U. deningeri*, and *V. vulpes*. Because our goal was to recognize the resource partitioning in adult animals, preference was given to sampling teeth that are among the last ones to develop, mineralize, and erupt (Linhart, 1968; Slaughter et al., 1974; Smuts et al., 1978). While preference was given to the teeth developing last, these were sometimes not available and alternative teeth were sampled.

The general method for stable isotope sampling of tooth enamel followed MacFadden and Cerling (1996) and Koch et al. (1997). For the tooth enamel, sampling involved drilling about 10–20 mg of pristine enamel powder off the tooth along a non-occlusal surface parallel to the growth axis and across its entire length using a 0.5 mm inverted cone carbide drill bit and a variable speed Dremel™ rotary tool. The powder was first collected and treated with 30% hydrogen peroxide for 24 h to remove organics. The hydrogen peroxide was then decanted and the enamel powder was then washed with distilled water, and soaked in 0.1 N acetic acid for another 24 h to remove any diagenetic carbonate. The following day the acetic acid was decanted and the enamel powder was washed with distilled water and dried.

After treatment, the samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Geology Department at the University of California, Davis. The ~1 mg samples were dissolved in 100% phosphoric acid at 90 °C to create CO_2. All samples were corrected to NBS-19 and UCD-SM92 an in-house marble standard. Precision for the samples was 0.1‰ for both carbon and oxygen.

Mean differences among species within localities were compared by ANOVA and post hoc Tukey HSD tests. Tukey HSD tests are similar to *t*-tests but take into account multiple comparisons. Statistical analyses were run on JMP IN 5 for students, with significance set at $p < 0.05$.

4. Results

Significant differences are observed in both carbon and oxygen isotope values among the three herbivore species (Appendix 1), forming two distinct groups (Fig. 4). All samples had carbon isotope ($\delta^{13}C$) values more negative than −10.0‰ indicating a habitat dominated by C_3 plants, similar to modern ecosystems in Spain (Collins and Jones, 1985). *C. elaphus* and *Equus* sp. form a separate group from *D. dama*. The mean carbon isotope values for *C. elaphus* (−11.4‰ ± 0.7‰; $n = 7$) and *Equus* sp. (−11.4‰ ± 0.5‰; $n = 4$) are the same, while the value for *D. dama* (−13.7‰ ± 0.3‰; $n = 2$) is more negative (Table 1). Opposite the carbon isotope results, the mean oxygen isotope ($\delta^{18}O$) values for *D. dama* are the most positive for the herbivores (−4.7‰ ± 0.4‰), while the mean values for *C. elaphus* (−8.4‰ ± 1.3‰) and *Equus* sp. caballine-type (−9.1‰ ± 1.7‰) are more negative.

Significant differences are also observed in $\delta^{13}C$ and $\delta^{18}O$ values among the six carnivore species (Appendix 1). For carbon, *U. deningeri* has the most negative mean $\delta^{13}C$ value (−15.2‰ ± 1.1‰; $n = 23$) and is significantly different from *P. leo* (−13.2‰ ± 0.4‰; $n = 6$) and *V. vulpes* (−12.2‰ ± 0.8‰; $n = 12$). All other taxa are statistically similar. Displaying the most positive mean $\delta^{13}C$ value for the carnivores was *C. lupus* ($n = 1$) with a value of −12.1‰ (Table 1). For oxygen, *V. vulpes* had the most positive mean $\delta^{18}O$ value at −4.8‰ ± 1.0‰ and was significantly different from all taxa except *C. lupus*. *C. lupus* is significantly different from *U. deningeri* and *P. leo*. *L. p. spelaeus* (−7.9‰ ± 0.3‰; $n = 2$) and *C. alpinus* (−8.1‰; $n = 1$) are similar to all taxa except *V. vulpes*. Displaying the most negative $\delta^{18}O$ value for the carnivores was *P. leo* with a value of −9.2‰ ± 1.1‰.

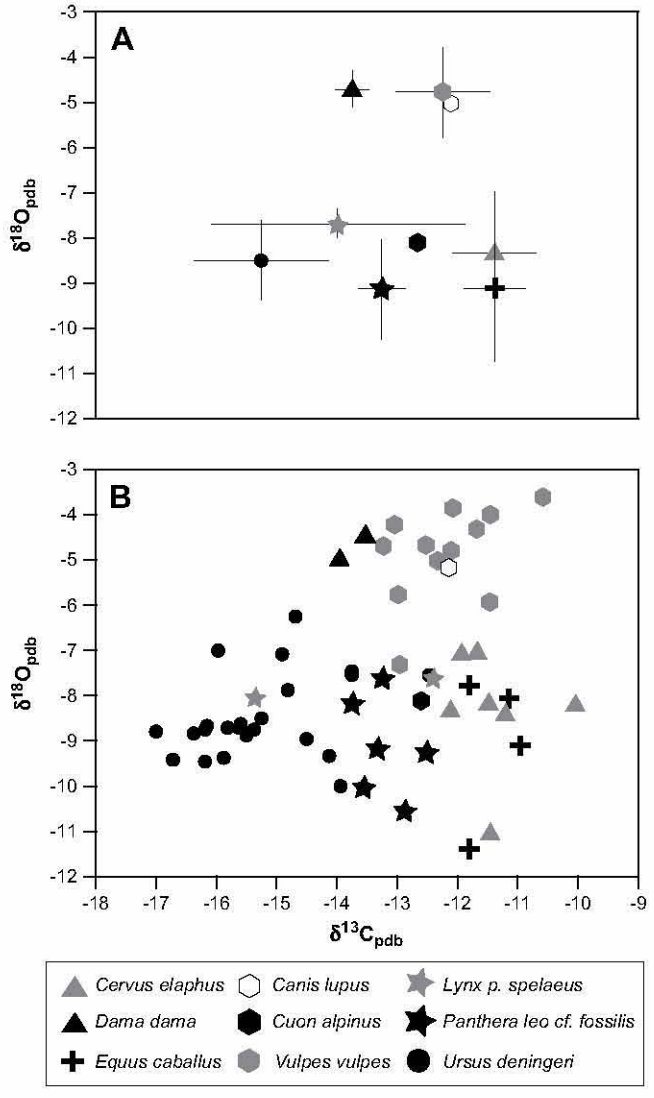

Fig. 4. (A) Mean isotopic values from tooth enamel for species analyzed within this study. Lines represent one standard deviation from the mean. (B) Individual isotopic values.

5. Discussion

5.1. Diagenetic evaluation

P. leo occurs and was analyzed from the three localities (TG, TD and SH), and similarly *V. vulpes* occurs and was sampled from TG and SH. While these localities likely had diverse depositional histories with fossil preservation taking place by different chemical processes, individuals of the same species had similar isotopic values. These data show that the enamel samples did not undergo diagenetic alteration, as the differences in preservational environment among the localities would likely have created differences in isotopic values. The data also support the idea of analyzing and comparing the ecology of species occurring within a particular faunal unit. Even though individuals may not have lived contemporaneously, species within ATA FU 6 appear to have maintained similar ecological relationships amongst themselves.

Table 1
Stable carbon and oxygen isotope values of large mammal species from the late Pleistocene deposits of the Sierra de Atapuerca, northern Spain.

Taxon	*N*	Mean $\delta^{13}C$ (‰)	$\delta^{13}C$ SD (‰)	Mean $\delta^{18}O$ (‰)	$\delta^{18}O$ SD (‰)
Average for All Specimens	58	−13.5	1.8	−7.6	1.9
Herbivores					
Artiodactyla					
Cervidae					
Cervus elaphus priscus	7	−11.4	0.7	−8.4	1.3
Dama dama clactoniana	2	−13.7	0.3	−4.7	0.4
Equidae					
Equus sp. (Caballine-type)	4	−11.4	0.5	−9.1	1.7
Carnivores					
Canidae					
Canis lupus	1	−12.1	–	−5.1	–
Cuon alpinus	1	−12.6	–	−8.1	–
Vulpes vulpes	12	−12.2	0.8	−4.8	1.0
Felidae					
Lynx p. spelaeus	2	−13.9	2.1	−7.9	0.3
Panthera leo cf. *fossilis*	6	−13.2	0.4	−9.2	1.1
Ursidae					
Ursus deningeri	23	−15.2	1.1	−8.5	0.9

5.2. Herbivore ecology

Differences in resource use and physiology are implied by the statistically significant differences in isotopic values detected among the taxa. The isotopic results generally conform to predictions based on what is known about the ecology of *C. elaphus* and *Equus* sp. *Cervus* and *Equus* sp. mean $\delta^{13}C$ values fall close together within the range expected for animals foraging in a light forest or grassland (Bocherens, 2003). The carbon isotope results for *C. elaphus* are not those expected from an indicator of closed forest at Pleistocene sites, as was suggested by some authors (Sommer and Nadachowski, 2006). Instead, the values obtained support the use of a more open, light forest or grassland environment for this cervid species. Although *C. elaphus* live mainly in forest areas and the adjacent surrounding fields today, it can also occupy open moorland (Staines et al., 1982). Similar to the results of Drucker et al. (2003), these results indicate that this species is likely more of a generalist capable of living and feeding in many different habitat types, and likely on many different forage types. The horse isotopic values match our predictions as a more generalist or mixed-feeder having values similar to *C. elaphus*.

Our predictions for carbon isotope values in *D. dama*, being indicative of more open habitats and $\delta^{13}C$ values more positive than *C. elaphus* and *Equus* sp., are falsified. Our data for *D. dama*, being significantly more negative than the *Equus* sp. and *C. elaphus* data, indicate that the two *D. dama* individuals sampled inhabited or at least foraged in more closed habitat than either the sampled *Equus* sp. and *C. elaphus* populations. While grasses, sedges, and rushes are a dominant part of the diet of modern *D. dama*, other plants and plant parts, including fruit and even bark, can make up a significant portion (>70%) of forage depending on where the population is located and what food is available at the time (Chapman and Chapman, 1975). These data show that *D. dama* was capable of living and eating in a wider variety of habitats than we expected. *D. dama* also differs from *C. elaphus* and *Equus* sp. in that it rarely drinks, obtaining most of its water from the vegetation it eats (Chapman and Chapman, 1975). The positive oxygen isotope values for *D. dama* conform to expectations for an animal that rarely drinks. Further, this ecology in *D. dama* (i.e., water from plant leaves) would support the idea of a Near East origin for the species, and its association with more arid Mediterranean environments.

5.3. Carnivore ecology

Similar to the herbivores, statistically significant differences were observed in carnivore $\delta^{13}C$ values implying resource partitioning. *U. deningeri* differed from the rest of the carnivores. Taking into account the isotopic differences in the enamel of predator and prey (Fox-Dobbs et al., 2006), the $\delta^{13}C$ values of all carnivores, except *U. deningeri*, fall among the range of $\delta^{13}C$ values observed at these localities, and are typical of what is expected for predators that are not specialized on a particular species, but tend to be more generalized or opportunistic. Without sampling smaller mammals, suggesting preference for one prey type over another would be unwise.

While we are aware that certain cave bear populations may not have been obligate herbivores (Stiner et al., 1998; Richards et al., 2008), the negative $\delta^{13}C$ values displayed by *U. deningeri* at Sima de los Huesos are similar to previous isotopic studies (Bocherens et al., 1991a, 1994), correspond to what has been proposed about their ecology from morphological analyses (García, 2003), and are suggestive of this population having an herbivorous diet. Physiologically, a long hibernation period with a strong contribution of lipids to metabolism, could also explain the low apatite $\delta^{13}C$ values observed in Pleistocene bears relative to coeval carnivores and herbivores (Bocherens et al., 1994).

Examination of oxygen isotope values in the carnivores shows that *C. lupus* and *V. vulpes* had significantly more positive oxygen isotope values compared to the other carnivores at this locality. While we cannot currently pinpoint why the $\delta^{18}O$ values are significantly more positive in these two species, the differences may result from utilizing a different water source. For example, these two species could be using a different watering hole or obtaining most of their water from prey. The positive $\delta^{18}O$ values could also be due to physiological differences compared to the other carnivores.

5.4. Implications for prehistoric human diet

Palaeodietary reconstruction using stable carbon and nitrogen isotope values from European Neanderthals has previously been analyzed from sites such as: Les Pradelles and Saint-Césaire I (France) (Bocherens et al., 1991b; Fizet et al., 1995; Bocherens and Drucker, 2003; Drucker and Bocherens, 2004), Scladina and Spy (Belgium) (Bocherens et al., 1999, 2001), Vindija (Slovenia) (Richards et al., 2000). Each of these investigations has suggested that the values of Neanderthals were similar to those of contemporary predators indicating that their diet was generally dominated by the meat of large herbivores. The results obtained within the present study provide a good framework in which to place ancient humans. In this context, based on these previous Neanderthal studies, we suspect that the dietary habits of the pre-Neanderthals (*H. heidelbergensis*) discovered in the Sima de los Huesos that lived during the Middle Pleistocene already had a trophic position similar to those of contemporary large predators, such as lions. We predict that future isotope analysis of this population would show values similar to the other large carnivores at the site.

5.5. Comparison with other Pleistocene sites

Comparison of the isotope data presented here from the Sierra de Atapuerca to other similarly sampled Pleistocene localities, such as Kent's Cavern, England (Bocherens et al., 1995), Marillac, France (Fizet et al., 1995), Paglicci Cave, Italy (Iacumin et al., 1997), Scladina Cave, Belgium (Bocherens et al., 1997), and Venta Micena, Spain (Pamlqvist et al., 2003, 2008), does not reveal overall generalities among the fauna in their resource use. However, it appears that

faunal relationships are dependent at least on geographic location as well as what particular species are present. Our results appear most similar to the results found at the Upper Pleistocene Kent's Cavern, England (Bocherens et al., 1995) than any of the other mentioned localities. While the exact same taxa were not present or sampled between Kent's Cavern and the Sierra de Atapuerca sites, both show that horses and cervids have $\delta^{13}C$ values near the most positive in the fauna, large carnivores display intermediate carbon isotope values, and bears show the most negative values. These results in comparing the faunas are interesting in that they show species' ability to interact differently when among various fauna at the different localities.

This study shows that isotopic analyses do not necessarily require ecosystems with C_3 and C_4 plants or the analyses of nitrogen isotopes (i.e. collagen) to be informative. Isotopic analysis of enamel apatite in C_3-dominated ancient ecosystems provides more detailed information about ancient human and faunal dietary habits, and the possible role of dietary changes during climatic oscillations. With the addition of more species, especially smaller mammals, we can obtain an even more complete understanding of the ecological setting in which humans lived and analyses over time will allow an understanding of how the environment and the ecology of species within the Sierra de Atapuerca, including humans, evolved over the last million years of the Pleistocene.

6. Conclusions

Significant differences in stable isotope values obtained from the tooth enamel of large carnivores and herbivores from the Middle Pleistocene in the Sierra de Atapuerca imply differences in resource use. The isotopic results generally conform to ecology indicated by other techniques in previous analyses. For the herbivores sampled, isotopic values support *C. elaphus* and *Equus* sp. as being mixed-feeders in a light forest or grassland, and *D. dama* foraging in more forested habitats.

For the carnivores, isotopic values are more negative in *U. deningeri* than the other sampled carnivores. We suspect that these negative values are either due to herbivory or effects from hibernation. The data for rest of the carnivores suggest the predators to be capable of feeding on a variety of prey and not specialized on a particular species. This technique provides another methodology to assess ecology of taxa and accurately portray the setting in which humans lived. Future analyses may allow an understanding of the evolution of ecology within the Sierra de Atapuerca over the last half of the Pleistocene.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jas.2008.12.018.

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